# Why do vulnerable mayflies thrive in trout streams?

Barbara L. Peckarsky, Andrea C. Encalada, and Angus R. McIntosh

There are many examples of aquatic insects that avoid ovipositing in risky habitats because their populations are decimated by vertebrate predation if they make mistakes. Stream-dwelling mayflies are not among those examples. In fact, some highly vulnerable mayfly species (e.g. Baetis spp.) preferentially oviposit and achieve higher densities in streams with the highest risk of vertebrate predation. Along with many students and other colleagues, we have spent many years trying to understand that perplexing pattern. Adaptive behavior and life history strategies that can be induced experimentally by predator risk result in equivalent probabilities of surviving the larval stage, but do not explain the high relative abundance of Baetis populations in streams with trout compared to those in fishless streams. Furthermore, non-consumptive effects of predators on prey behavior and life history may have a greater influence on the rate of Baetis population growth than does consumption by trout. The key piece of the puzzle for Baetis to achieve high densities in trout streams is that females preferentially oviposit in trout streams, because those streams have greater availability of optimal oviposition sites (large rocks that protrude from the water surface during the brief flight period). Intriguingly then, competing selection pressures independent of predation risk (hydro-geomorphology that maximizes hatching success) may explain why Baetis mayflies selectively oviposit in trout streams. Consequently, increasing frequency of extreme hydro-geomorphological events associated with climate change may threaten the ability of these important mayflies to sustain populations.

Downloaded from http://academic.oup.com/ by guest on April 29, 2016

## Background

There are numerous examples among the insects of the "Mother Knows Best" hypothesis; that is, females should oviposit in habitats that increase the probability that their offspring will prosper (Kouki 1991; Thompson and Pellmyr 1991; Price et al. 1998). Nonetheless, selective oviposition is not universal among insect species, and may depend on the mobility of larvae. For example, Bryant (1969) argued that holometabolous species should be more selective of oviposition sites, because their larvae tend to be more sedentary than those of hemimetabola, whose more mobile larvae are capable of correcting their mothers' mistakes. In fact, selective oviposition and associated superior performance of offspring have been well documented among the terrestrial herbivorous holometabola (Thompson 1988; Craig et al. 1989; Ohgushi 1992; Price 1994, Price and Ohgushi 1995; Sadegui and Gilbert 1999).

Alternatively, females of many species of insects oviposit at locations that minimize egg predation, egg parasitism, or environmental stress on eggs (e.g. desiccation) (Rausher 1979; Otto and Svensson 1981; Damman and Cappucino 1991; Canyon et al. 1999; Juliano et al. 2002; Wissinger et al. 2003). In other cases, oviposition behavior has been shown to minimize pre-oviposition mortality of females (Michiels and Dhondt 1990; McMillan 2000). Viewed in this context, oviposition behavior is an adaptive trait that can fundamentally influence population dynamics of insects (Ohgushi 1995; Resetarits 1996; Spencer et al. 2002).

In contrast to the well-documented cases supporting the contention that mothers of terrestrial insect species know best, entomologists have generally considered females of aquatic insects to be non-selective in their oviposition behavior (e.g., Hinton 1981), thereby not conforming to the "Mother Knows Best" hypothesis. However, there is convincing evidence of selective oviposition among not only aquatic holometabola, but also aquatic hemimetabolous insects. For example, females of some Odonata (Libellulidae) "taste" the water and avoid laying eggs in aquatic habitats with vertebrate predators (Wildermuth 1992). Other Odonata (Coenagrionidae) females lay eggs at locations in streams with optimal current, which results in higher hatching success (Siva-Jothy et al. 1995). Many species of Trichoptera oviposit underneath large, stable rocks emerging from the water surface, which increases egg survival by reducing

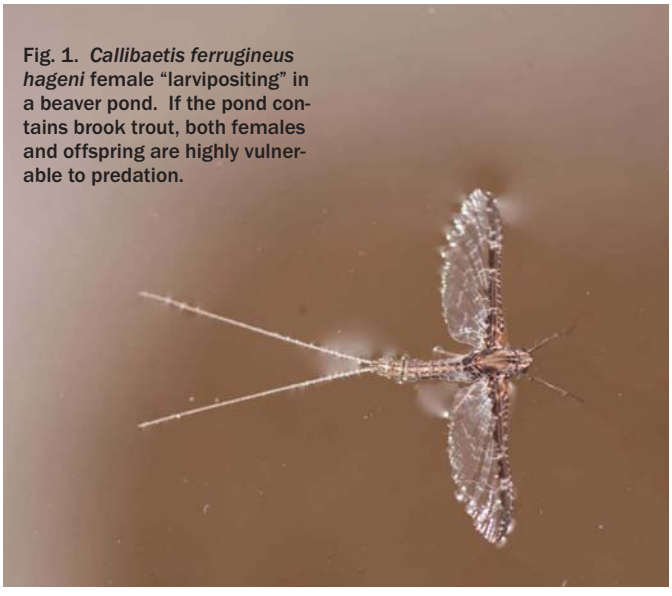


Fig. 1. *Callibaetis ferrugineus hageni* female "larvipositing" in a beaver pond. If the pond contains brook trout, both females and offspring are highly vulnerable to predation.

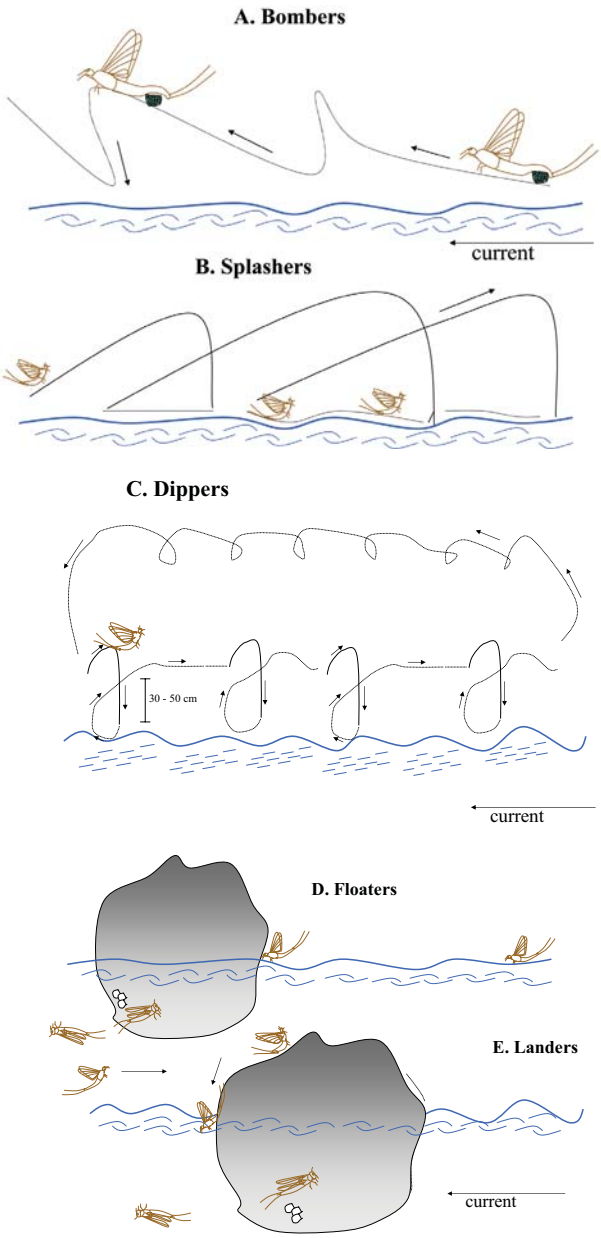



Fig. 2. Oviposition behaviors of different mayflies (Ephemeroptera) observed in the Upper East River drainage basin, near the Rocky Mountain Biological Laboratory in western Colorado. A. Splashers (e.g., *Siphlonurus occidentalis*); B. Bombers (e.g., *Drunella doddsi*); C. Dippers (e.g., *Rhithrogena hageni, Diphetor hageni, Epeorus longimanus*); D. Floaters (e.g., *Acentrella turbinae*); and E. Landers (e.g., *Baetis bicaudatus*). (Modified from Encalada and Peckarsky 2007.) Supplementary material available to authorized users in the online version of this article (doi:10.1007/s00265-007-0376-4) includes an S1 PowerPoint presentation showing animations of oviposition behaviors of the different mayflies. To activate the animations, click on "ppt presentation" or the F5 key, and use the "return" key to move through the different animations (PPT 232 KB).

scouring and damage associated with rock movement (Reich and Downes 2003). Aquatic Coleoptera (Hydrophilidae) females avoid laying eggs in ponds with predatory fish (Resetarits 2001). Aquatic Diptera, especially Culicidae, selectively oviposit in locations that protect their offspring by not only by minimizing predation and competition from potential competitors, but also by maximizing food resources (Blaustein and Kotler 1993; Canyon et al. 1999). Most extraordinary behaviors are exhibited by some Hemiptera (Belostomatidae) (Smith 1976), whose females oviposit on the hemelytra of

Downloaded from http://ae.oxfordjournals.org/ by guest on April 29, 2016



Fig. 3. *Baetis bicaudatus* female imago.



Fig. 4. *Baetis bicaudatus* female imago ovipositing on the underside of a rock in the East River. The egg mass is to her right.

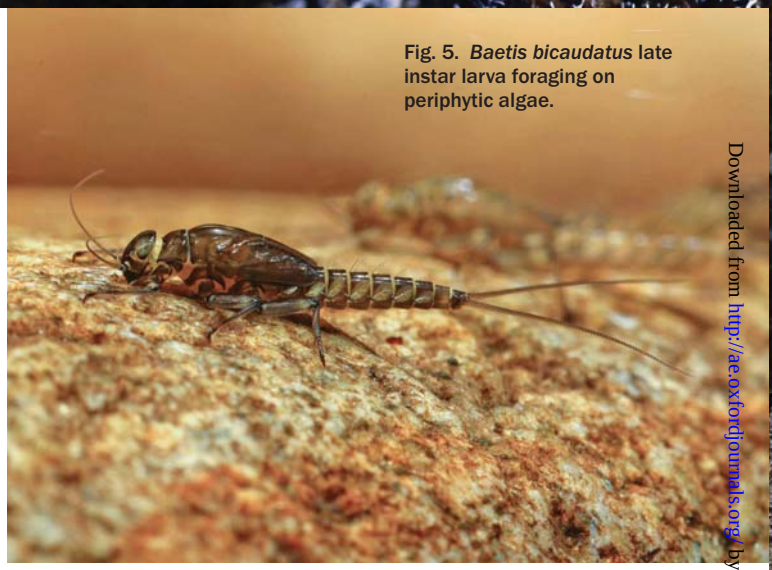


Fig. 5. *Baetis bicaudatus* late instar larva foraging on periphytic algae.

males who then brood their eggs until hatching. Therefore, female insects that oviposit in water may also know best.

That being said, Ephemeroptera are the most perplexing group, having examples of totally negligent mothers (e.g., Caudill 2003) and those that risk their lives (and those of their babies) to carefully select habitats for oviposition (e.g., Encalada and Peckarsky 2006). Despite larvae having essentially 100% mortality in beaver ponds containing brook trout, ovoviviparous *Callibaetis* mothers (Fig. 1), which incubate their eggs until they are ready to hatch (highly unusual behavior for mayflies), do not avoid "larvipositing" in such dangerous places, and larvae have no apparent predator-avoidance behaviors (Caudill and Peckarsky 2003). Caudill (2003) argues that this genus of mayflies has evolved to exploit ephemeral habitats, and thereby explains the negligence of mother *Callibaetis* by phylogenetic inertia (Caudill and Peckarsky 2003).

In fact, most mayflies do not precisely control the destination of their eggs. Encalada and Peckarsky (2007) have described five functional categories of mayfly oviposition behaviors in streams (based on observations and published literature: (Needham et al. 1905; Brittain 1982; Elliott and Humpesch 1983), four of which are seemingly reckless (Fig. 2 A, B, C, D). For example, Ephemerellidae females drop their eggs into the water while flying near the surface (A); Ameletidae females oviposit by splashing on the water surface and releasing all their eggs (B); Heptageniidae females dip their abdomens on the water surface repeatedly, releasing a few eggs at a time (C); and some Baetidae float downstream while releasing their eggs, or if they contact a large rock, they crawl underneath to oviposit (D). Pre-oviposition mortality of adult females varies according to their behavior, with the groups making more contact with the water surface having the highest probability of drowning or being eaten by brook trout before ovipositing (Encalada and Peckarsky 2007). Furthermore, females flying near the water (even the ones that do not touch the water surface to oviposit) were highly susceptible to aerial predators.

### How smart are mayfly mothers?

Among the mayflies, one genus stands alone, exhibiting a remarkably selective oviposition behavior perhaps unexpected for such a primitive group (Fig. 2E). *Baetis* females (Fig. 3) fly directly to the upper surfaces of rocks protruding from the water, then crawl underwater on the downstream side of the rock to oviposit on the underside (e.g. Morgan 1911; Murphy 1922; Bengtsson 1982; Peckarsky et al. 2000) (Fig. 4). As first described most eloquently by Eaton (1888; p. 11):

> "... she creeps down into the water—enclosed within a film of air, with her wings collapsed so as to overlie the abdomen in the form of an acute narrowly linear bundle, and with her setae closed together—to lay her eggs upon the underside of stones, disposing them in rounded patches, in a single layer evenly spread, and in mutual contiguity. The female on the completion of her labour usually floats up to the surface of the water, ineffectively swimming with her legs, and, on emerging, her wings all at once are suddenly unfolded and erected; she then either flies away, or (as often happens) if her setae have chanced to become wet and cannot be extricated from the water, she is detained by them until she is drowned. In some instances, however, the female dies under water beside her eggs."

*Baetis* larvae (Fig. 5) are highly mobile algae-grazers and graceful swimmers that are capable of selecting their own optimal foraging habitat (Kohler 1984; Richards and Minshall 1988; Peckarsky 1996). Therefore, we would expect stronger selection on *Baetis* oviposition behavior to minimize female pre-oviposition mortality and maximize egg survival than to maximize offspring performance. Most *Baetis* females recovered in brook trout guts had already laid their eggs (average ~80%), thereby reducing losses of pre-oviposition

Downloaded from http://ae.oxfordjournals.org/ by guest on April 29, 2016



Fig. 6. Underside of a rock turned over in the East River containing hundreds of *Baetis bicaudatus* egg masses.



Fig. 7. Close-up of *Baetis bicaudatus* egg masses showing newly oviposited ones (lower left, bright white color), more mature egg masses (cream-colored), and some eggs that have hatched within the more mature egg masses (brighter cream color with less definition).

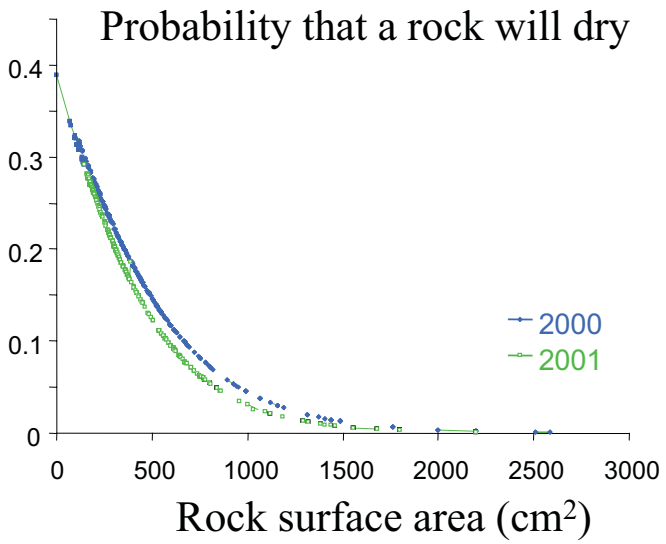



Fig. 8. Relationship between rock area and probability of drying, from logistic regression models for rocks protruding from the water surface of the East River during the summers of 2000 and 2001 (Modified from Encalada and Peckarsky 2006.)

females to fish predation. Females with oviposition strategies that did not touch the water surface had the lowest risks of fish predation before ovipositing (Fig. 2A); and females with longer exposure to the water surface had the highest pre-oviposition predation rates (Fig. 2B and D). Nonetheless, *Baetis* oviposition behavior was not without risk in terms of fish predation, and had the highest risk of pre-oviposition predation while flying near the water surface (Encalada and Peckarsky 2007). Therefore, it does not appear that such specialized oviposition behavior evolved to reduce the probability of pre-oviposition mortality.

Alternatively, the strategy of carefully attaching eggs to the undersides of rocks does appear to increase the probability of egg survival (Peckarsky et al. 2000; Encalada 2005). *Baetis* females are attracted by highly reflective splash and thereby selectively oviposit under large rocks located in high-velocity current (Encalada and Peckarsky 2006) (Fig. 6). *Baetis bicaudatus* eggs require 14 days of incubation before hatching (Fig. 7). Preferred substrates have a high probability of persistent flow, thereby minimizing egg desiccation, which could provide a strong selection pressure for females to oviposit under



Fig. 9. Brook trout (*Salvelinus fontinalis*).

Downloaded from http://ae.oxfordjournals.org/ by guest on April 29, 2016



Fig. 10. The East River near the Rocky Mountain Biological Laboratory in western Colorado. Contains breeding populations of brook trout.

rocks with lower probability of drying (Fig. 8). Thus, *Baetis* mothers perhaps know enough to deliberately place their eggs in locations that maximize hatching success (Peckarsky et al. 2000). After that, the larvae are left to their own devices.

Given how potentially dangerous it is for *Baetis* females to oviposit in trout streams, the next most logical question is whether they avoid making such mistakes, unlike their cousins (*Callibaetis*). High-elevation montane and subalpine streams in the Upper East River drainage basin of western Colorado are known to support breeding populations of brook trout (*Salvelinus fontinalis*) (Fig. 9), which was introduced from eastern North America in the mid to late 1800's. Other streams in this drainage basin (mostly headwater streams) are completely fishless because waterfalls act as barriers to

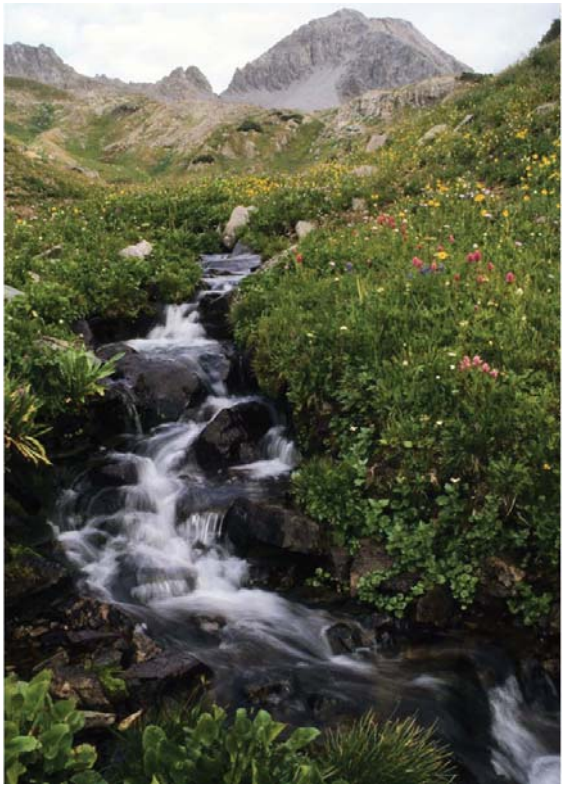


Fig. 11. An unnamed fishless stream draining the basin southwest of Snowmass Mountain in western Colorado.

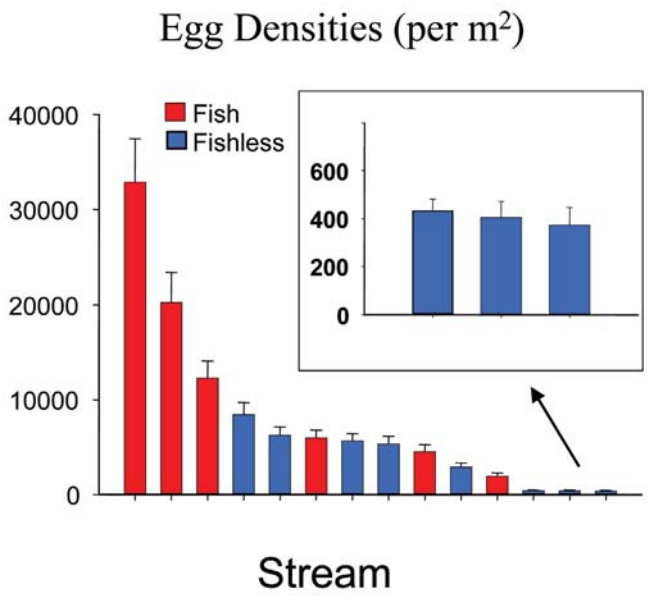



Fig. 12. Egg densities (eggs/m²) of the 2001 and 2002 cohorts of *Baetis bicaudatus* estimated from counts of egg masses on rocks protruding from fish (red) and fishless (blue) streams in the Upper East River drainage basin in western Colorado. Error bars represent confidence intervals around mean estimates of egg densities obtained from size-fecundity regressions of females. (Modified from Encalada and Peckarsky [in press] or Encalada 2005.)

upstream dispersal of trout. (Figs. 10 and 11) Contrary to expectations based on evolution of predator avoidance behaviors, we have learned from many hours of turning over rocks and counting eggs in multiple trout streams and fishless streams that not only do female *Baetis* not avoid laying eggs in trout streams, but also more females lay eggs in trout streams than in fishless streams (Fig. 12) (Encalada and Peckarsky, in press). (Fig. 13)

### How do larvae cope with mom's bad decisions?

While we know that laying eggs in trout streams is risky for the ovipositing females, the next generation of larvae face even bigger



Fig. 13. Andrea Encalada painstakingly counting *Baetis* egg masses that had been oviposited under a large rock that was protruding from the East River.

Downloaded from http://ae.oxfordjournals.org/ by guest on April 29, 2016



Fig. 14. Larva of *Baetis* species B, which grows and develops during baseflow periods at this elevation, and is thereby more vulnerable to trout predation.

problems while attempting to forage on periphyton algae resources, grow, and develop to reproductive maturation. We used time series of collections of *Baetis* larvae for several generations in streams of the Upper East River drainage basin to calculate and compare larval mortality between fish and fishless streams. Not surprisingly, larval mortality of the species of *Baetis* (Fig. 14) that grows and develops during baseflow conditions when risk of trout predation is the highest (Peckarsky et al. 2001) was significantly higher in trout streams than in fishless streams (Fig. 15) (Peckarsky et al. 2008). Therefore, female *Baetis* are placing their offspring at much greater risk by preferentially ovipositing in trout streams.

Moreover, both male and female *Baetis* that survive potential predation by trout nevertheless incur a significant cost by maturing at smaller sizes in fish streams than in fishless streams (Fig. 16) (Peckarsky et al. 2001). *Baetis*, as all other mayflies, have indeterminate growth, thereby not having a fixed number of instars

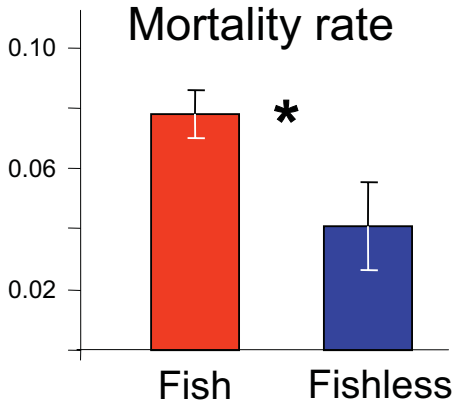



Fig. 15. Mean (± SE) mortality of *Baetis* species B that develops through its larval stage during baseflow when trout predation is highest. Mortality (*R* = loss rates) estimated from the slopes of ln(density +1) larvae regressed against time for fish (red) and fishless (blue) streams. * = significant difference between fish and fishless streams. (Modified from Peckarsky et al. 2008.)

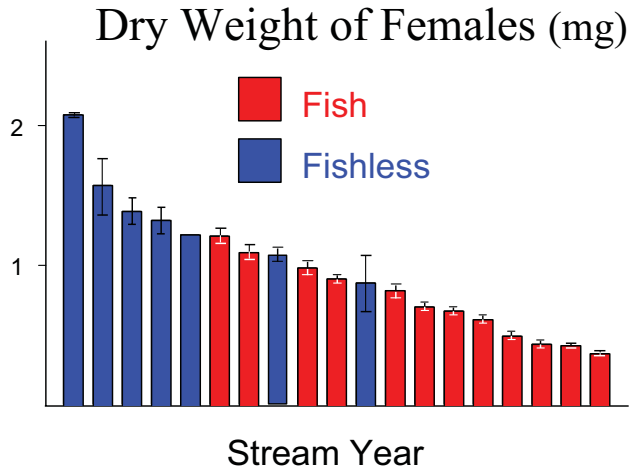



Fig. 16. Mean (± SE) dry weight (mg) of mature female *Baetis* species B larvae from fish (red) and fishless (blue) streams sampled from 1994 to 1996 in the Upper East River drainage basin. (Modified from Peckarsky et al. 2001.)

through which they must develop before metamorphosing. Instead, they exhibit flexible patterns of growth, molting, and reproductive development that are sensitive to environmental variation (Harker 1989). Consequently, given the appropriate environmental cues, *Baetis* females can alter their developmental pathways. We were able to induce accelerated development in two *Baetis* species by introducing brook trout chemical cues into experimental arenas (Peckarsky and McIntosh 1998) and, most astoundingly, entire fishless streams (Peckarsky et al. 2002a). Therefore, patterns of size distributions of *Baetis* observed in natural fish and fishless streams could be attributed to phenotypic plasticity induced by risk of trout predation, rather than by size-selective predation by trout (Allan 1978).

As is the case for many other insects, smaller females are less fecund (Fig. 17) (Peckarsky et al. 1993). As a result, the costs of

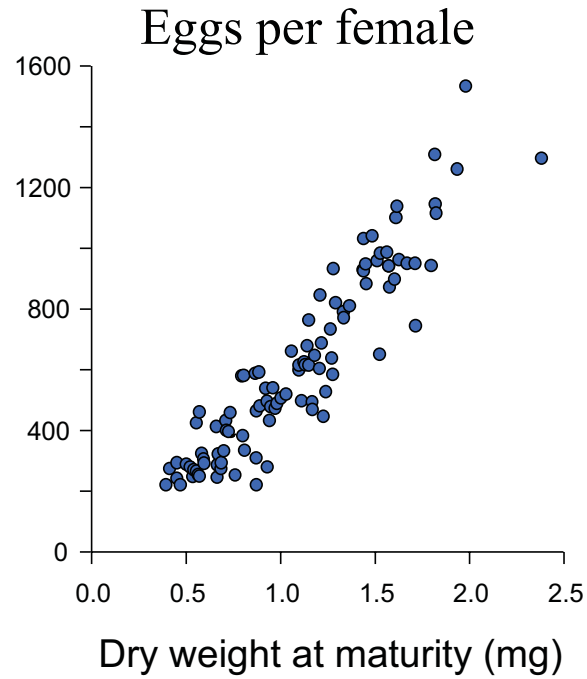



Fig. 17. Relationship between size (mg dry weight) of mature female larvae and fecundity (the number of eggs per female). (Modified from Peckarsky et al. 1993.)

Downloaded from http://ae.oxfordjournals.org/ by guest on April 29, 2016



Fig. 18. *Baetis bicaudatus* male imago. Note clear wings and large turbinate eyes.

predator-induced changes in development (smaller, less fecund females) are very large in terms of contributions of individuals to the next generation. In fact, such non-consumptive effects of predators reduce *Baetis* rates of population growth much more dramatically than actual consumption by predators (McPeek and Peckarsky 1998). However, there is no evidence that smaller male *Baetis* have lower fitness than large males. In fact, collections of copulating pairs of *Baetis* showed that males of intermediate size get more matings, which argues for balancing selection on male body size (Peckarsky et al. 2002b) (Fig. 18).

Despite the clear consumptive and non-consumptive costs of coexisting with predatory trout, analysis of many years of invertebrate samples from fish and fishless streams have corroborated the unexpected observation that *Baetis* achieves higher densities in trout streams than fishless streams. Not only do females fail to avoid ovipositing in the most dangerous places, but the offspring also appear to thrive, even though they are highly vulnerable to predation and incur a cost to fecundity if they survive their larval stage in trout streams (Fig. 19) (Peckarsky et al. 2008). So, how do they do that?

First, we know that larval development times are shorter in trout streams, which compensates in part for higher mortality rates (Fig. 20) (Peckarsky et al. 2008). Thus, predator-induced accelerated

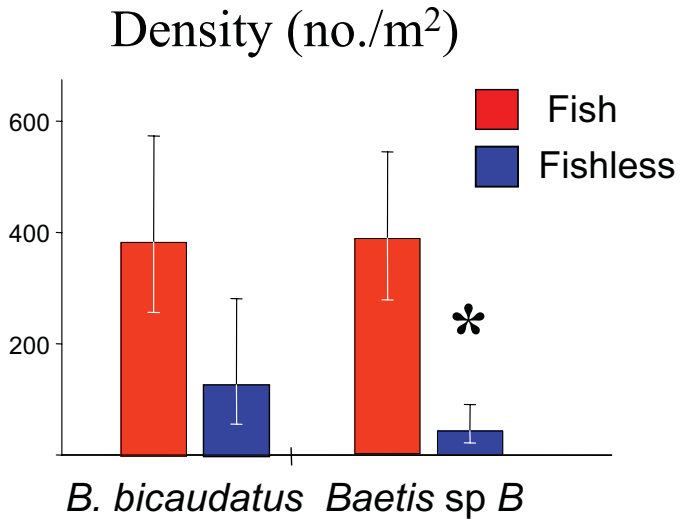



Fig. 19. Mean densities of two *Baetis* species (number per $m^2$) in fish (red) and fishless (blue) sites in the Upper East River drainage basin sampled summers 1994–1996 ± back-transformed upper and lower 95% confidence limits of ln(X+1) transformed densities. * = significant difference between fish and fishless streams. (Modified from Peckarsky et al. 2008.)

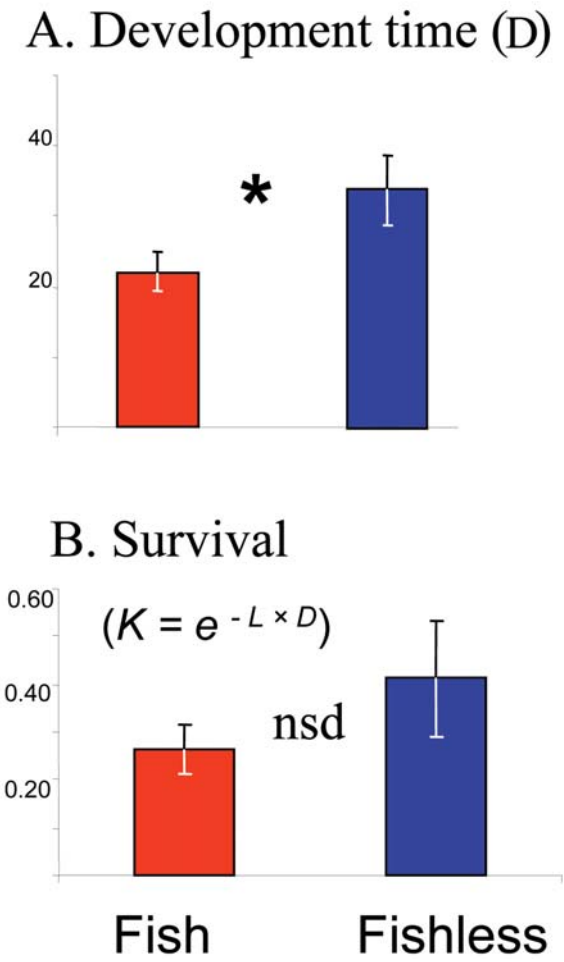



Fig. 20. Mean (± SE) A. Development times (*D*: days to develop from stage II to stage IV larvae: see Fig. 26 for illustration of *Baetis* stages), and B. Probability of surviving the larval stage ($K = e^{-RD}$, where $R$ = loss rates, see Fig. 15) of *Baetis* species B from 1994–1996 cohort abundance time series data in fish (red) and fishless (blue) stream sites in the Upper East River drainage basin. * = significant difference between fish and fishless streams; nsd = no significant difference. (Modified from Peckarsky et al. 2008.)

Downloaded from http://ae.oxfordjournals.org/ by guest on April 29, 2016

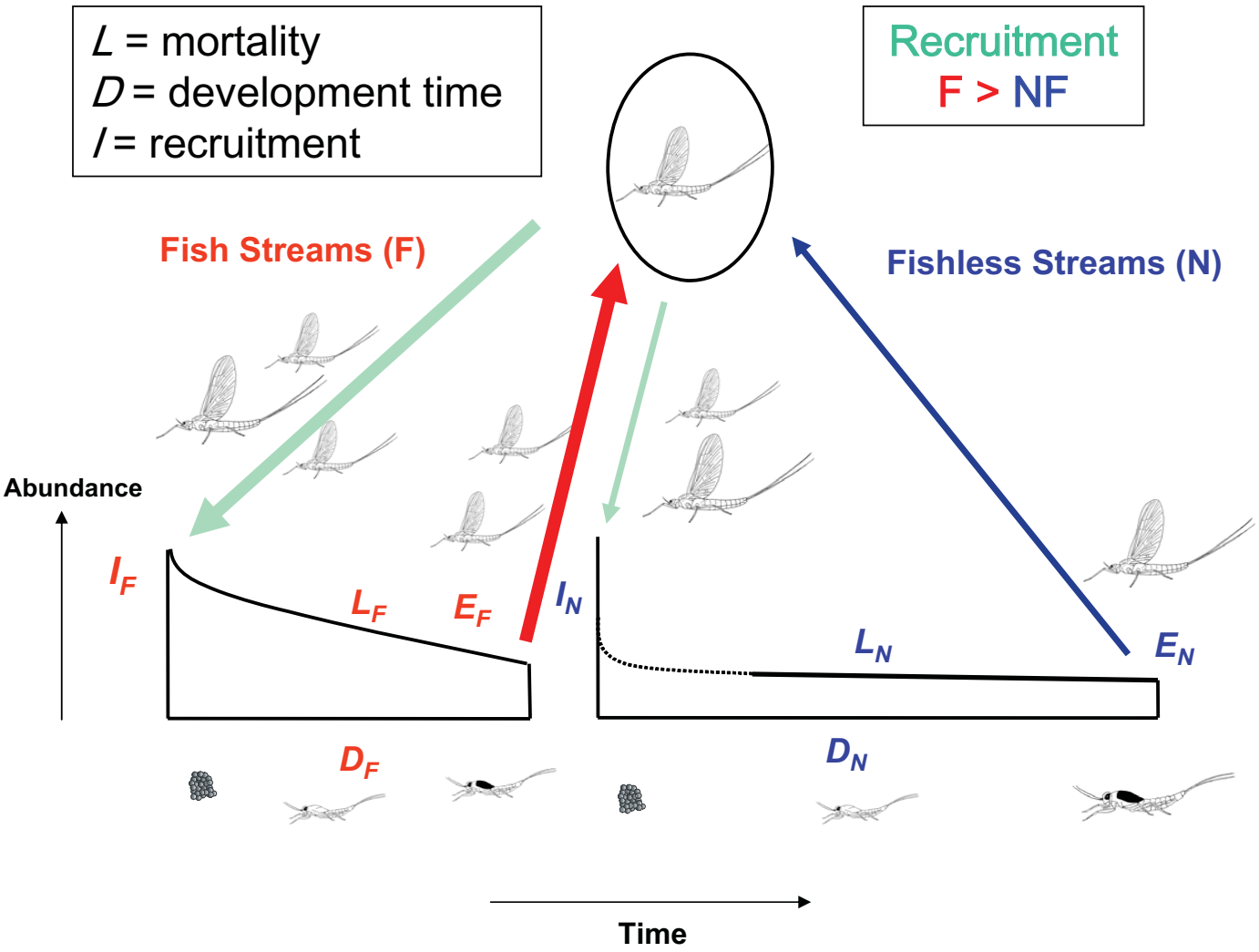



Fig. 21. Conceptual overview of potential influence of recruitment (*I*), loss rates ($L_F > L_N$) and development times (from stage II–IV: $D_N > D_F$) to explain higher densities of *Baetis* species B in fish than fishless streams ($E_F > E_N$). More mayflies emerged from fish ($H_F$) than fishless ($H_N$) stream habitats ($E_F \times H_F > E_N \times H_N$) and entered a regional pool of adults (circled). More mated females disperse to fish streams to oviposit ($I_F > I_N$). (Modified from Peckarsky et al. 2008.)

development results in similar probabilities of surviving the larval stage in fish and fishless streams (Peckarsky et al. 2001). *Baetis* individuals who respond to predators by accelerating their larval stage thereby reduce time spent in a dangerous habitat. Although smaller individuals sacrifice fecundity, smaller larvae are also less vulnerable to predation by trout (Allan 1978, 1981). In fishless streams, mortality is lower and individuals extend their larval stage, achieving larger sizes at maturity and higher fecundity. Thus, *Baetis* has evolved life history plasticity that is adaptive and can be induced by "essence of brook trout" (Peckarsky et al. 2002a).

Although adaptive development results in similar probabilities of *Baetis* larval survival in fish and fishless streams, thereby explaining why females do not avoid ovipositing in trout streams, it does not explain why larvae thrive in more dangerous habitats. We have proposed a demographic model that may explain how such vulnerable mayflies can achieve higher densities in trout streams than in fishless streams (Fig. 21) (Peckarsky et al. 2008). For the second and final piece of the puzzle, we return to the oviposition story. More *Baetis* females oviposit in trout streams than in fishless streams (Fig. 12). Adding that piece of information to our demographic model, if more eggs are laid in trout streams, recruitment of new individuals (births) is higher in fish than in fishless streams. Thus, population

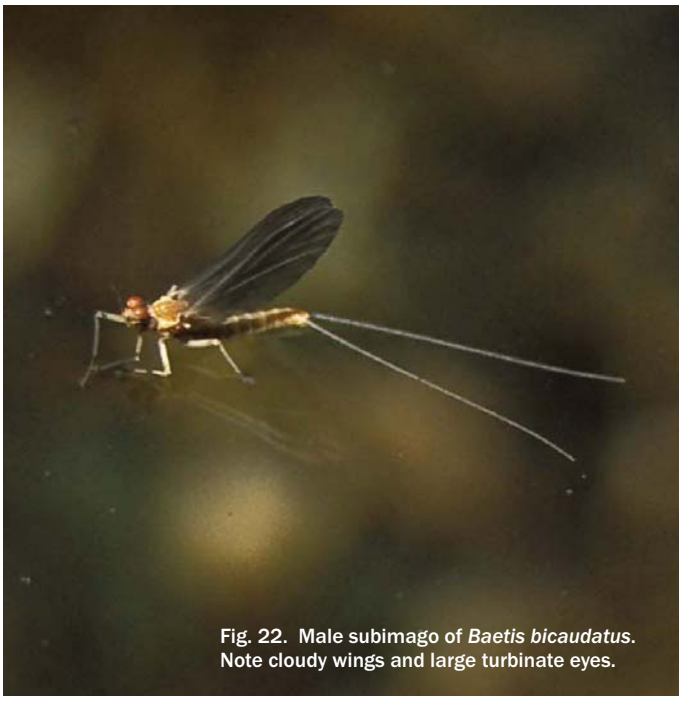


Fig. 22. Male subimago of *Baetis bicaudatus*. Note cloudy wings and large turbinate eyes.

Downloaded from http://ae.oxfordjournals.org/ by guest on April 29, 2016



Fig. 23. Large swarm of *Baetis bicaudatus* males in a clearing of Virginia Basin near RMBL.



Fig. 24. Copulating pair of *Baetis bicaudatus*. The male is underneath the female.

Downloaded from http://ae.oxfordjournals.org/ by guest on April 29, 2016

levels start higher in trout streams, and while they decline faster (loss rates are higher), shorter development times result in higher numbers of mature individuals emerging as adults.

Finally, we need to address why females prefer to lay eggs in trout streams. Individuals in the subimago stage (Fig. 22) that emerge from streams fly to riparian trees to undergo their final molt to the imago stage (Figs. 3 and 18). This transition takes about 48 hours for *Baetis bicaudatus*. Male imagoes form mating aggregations of various sizes and distances from streams, often swarming in clearings above distinct swarm markers (Peckarsky et al. 2002b) (Fig. 23). Females flying near swarms are intercepted by males, and copulating pairs drop to the vegetation to mate (Fig. 24). Males and females then fly off, and females fly back to streams to oviposit. We know that females do not have site fidelity, and that they disperse (primarily upstream) before ovipositing (Peckarsky et al. 2000). Recall that *Baetis* females are attracted by splash to large rocks protruding from the water surface. The reason more eggs are oviposited in trout streams is because the availability of those optimal substrates is higher in trout streams (Encalada 2005). Therefore, recruitment is not deterred by risk of predation but is limited by the distribution and abundance of the best rocks.

We conclude that *Baetis* thrives in trout streams because those streams have better oviposition sites, hatching success is high due to low post-oviposition, pre-hatching mortality, and accelerated development compensates in part for increased mortality on larvae from trout predation.

We find it most intriguing that a critical step in the life cycle of *Baetis* is driven by a hydro-geomorphological habitat constraint, and not by avoidance of predation. *Baetis* adults are very short-lived (1–4 days) (Peckarsky et al. 2002b), and thus successful recruitment relies on the synchrony between the precise timing of emergence, which is controlled by stream water temperatures (Fig. 25) (Harper and Peckarsky 2005), and by the availability of optimal rocks that are protruding from the water surface and will not dry in 14 days (Fig. 26). The period for successful oviposition can be a very narrow window of time. The water levels of streams in the Upper East

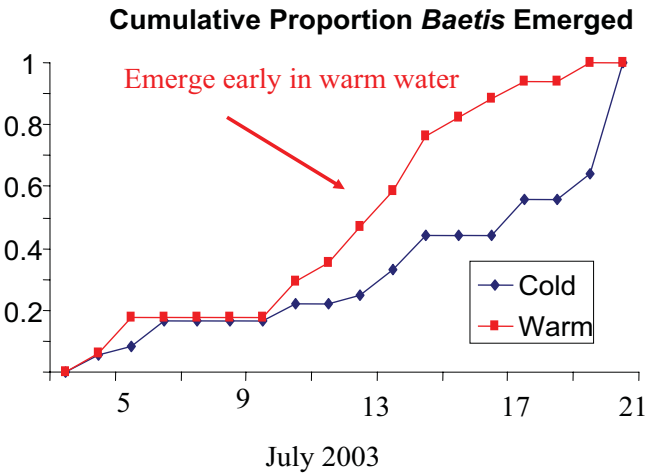



Fig. 25. Cumulative relative frequencies of *Baetis bicaudatus* emerging from warmed and ambient temperature treatments of a 5-week microcosm experiment carried out in summer 2003. Artificially warming the water in experimental units by ~ 2.5 °C significantly accelerated emergence of *Baetis* (K-S test: $D = 0.543$, $n = 17$, one-sided $P = 0.018$). (Modified from Harper and Peckarsky 2006.)

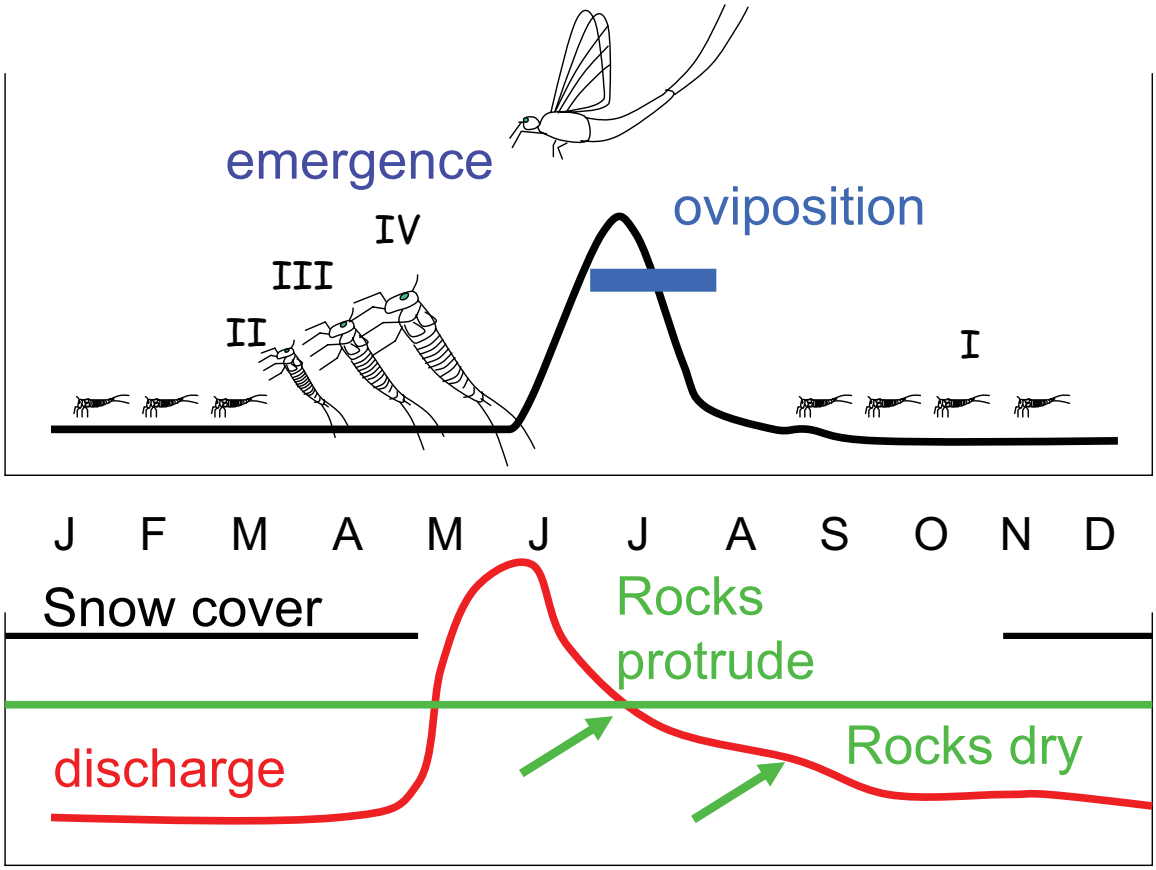



Fig. 26. Upper panel depicts the development of life stages of *Baetis bicaudatus* through time (horizontal axis) from overwintering stage I larvae (no wing pads), which begin to develop through stages II (wing pads wider than long), stage III (wing pads elongate and egg development begins) to the final non-feeding larval instar (IV), which lasts only 24 h and has large, blackened wing pads and fully developed eggs (Fig. 27). Stage IV larvae were used to estimate the size of mature larvae (Fig. 16) and the size-fecundity relationships (Fig. 17). (*Baetis* species B has the same pattern of development, but its phenology is delayed by approximately one month.) The vertical axis represents the spatial vertical dimension (larvae are aquatic and adults are terrestrial). The precise phenology of emergence during summer months (solid black line) depends on the amount of snow and ice cover and the timing of spring thaw (depicted in the lower panel). Adults are very short-lived (1–4 d), and have a narrow window of time for mating, dispersal, and oviposition (horizontal blue bar), which must coincide with the availability of optimal oviposition sites (depicted in green): protruding rocks that will not dry during the 14d period needed for incubation of eggs before hatching. The timing of emergence must thereby coincide with the descending limb of the annual stream hydrograph (discharge depicted in red), and be completed before baseflow is achieved (when the hydrograph flattens).



Fig. 27. Last larval instar of *Baetis bicaudatus* with blackened wing-pads (stage IV).



Fig. 28. Section of the East River south of Vera Falls near RMBL during high flow. No rocks protruding from the water surface.

Downloaded from http://ae.oxfordjournals.org/ by guest on April 29, 2016



Fig. 29. Same section of the East River as in Fig. 28, but at baseflow with many large rocks protruding from the water surface.

River drainage basin are very high after snowmelt (Fig. 28) and then decline to baseflow throughout the snow and ice-free period (Fig. 29). Furthermore, the window of time when good oviposition substrates are available is variable in both time (between years) and space (between streams) (Fig. 30). Thus, successful oviposition depends on the flow regime and can be disrupted by a potential mismatch between emergence and oviposition times (Peckarsky et al. 2000). Furthermore, females risk further danger from aerial predators and potentially harsh physical conditions if they must fly long distances to find suitable oviposition sites.

### Broader implications

Given the critical role of hydro-geomorphological constraints in explaining the ability of *Baetis* to sustain high population densities in trout streams, there are potentially dire consequences if human-accelerated environmental change alters the natural flow regime, and thus threatens these populations. As in other ecosystems, we have observed an increase in extreme hydrologic events (e.g., floods, droughts) associated with climate change that most certainly alters the natural flow regime of streams (McKnight 2001). For example, 2007 was an extremely dry year with early snowmelt and low stream flows; 2008 was the highest snow year and subsequently high water year on record (Fig. 31) (Fuller and Peckarsky 2011). Such hydrological anomalies juxtaposed in consecutive years have the potential to influence the already narrow seasonal window of time for short-lived *Baetis* females to oviposit when rocks are exposed and will provide good habitat for 14 days before desiccating.

In summary, optimal oviposition habitat is limited not only spatially (among streams) due to differences in hydro-geomorphology, but also temporally driven (within seasons and between years) by variation in climate and its effects on hydrological cycles. Therefore, while specialized oviposition behavior is a key component to explaining why these vulnerable mayflies thrive in trout streams, human-accelerated variation in the availability of quality oviposition

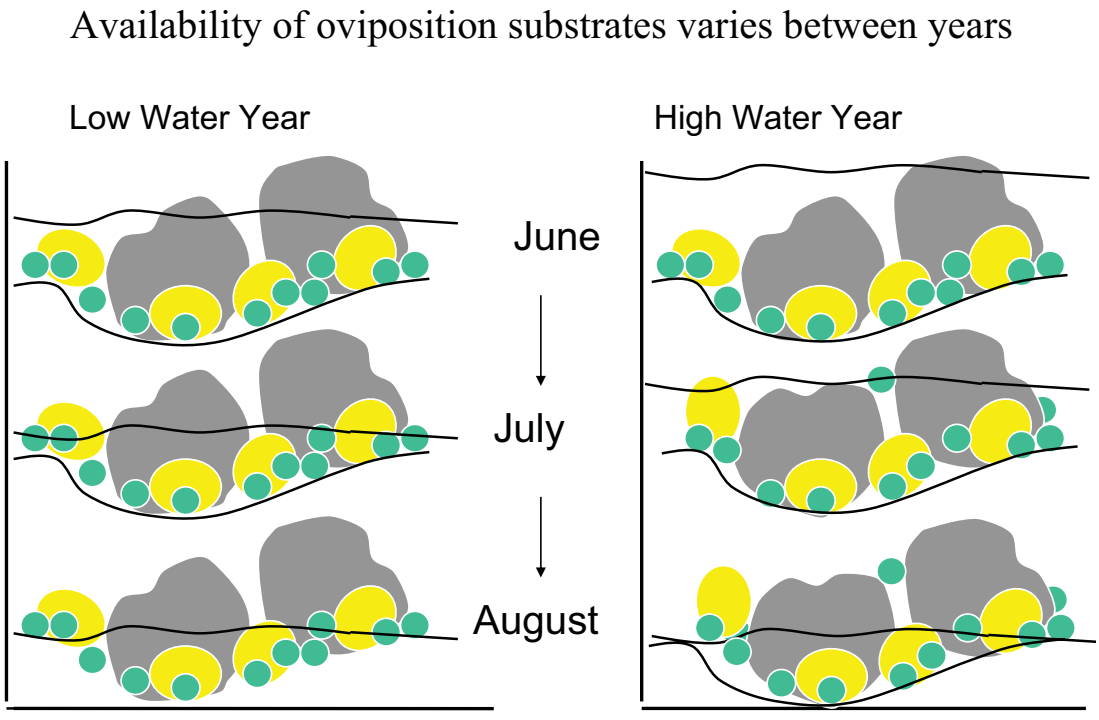



Fig. 30. Illustration of how the availability of oviposition sites varies seasonally and among years, depending on the amount of snow and ice cover, the timing of spring thaw, and subsequent protrusion of optimal rocks (gray) that are large enough to be stable and will not dry in 14d. Left panel represents a low-water (early) year, right panel a high-water (late) year, and the vertical dimension is time from early summer (top) to late summer (bottom). The horizontal dimension is space. Yellow and green "rocks" are suboptimal oviposition sites because they are relatively unstable (Peckarsky 1991) and rarely protrude from the water surface; of if they protrude, they dry before *Baetis* eggs can complete incubation to hatching.

Downloaded from http://ae.oxfordjournals.org/ by guest on April 29, 2016

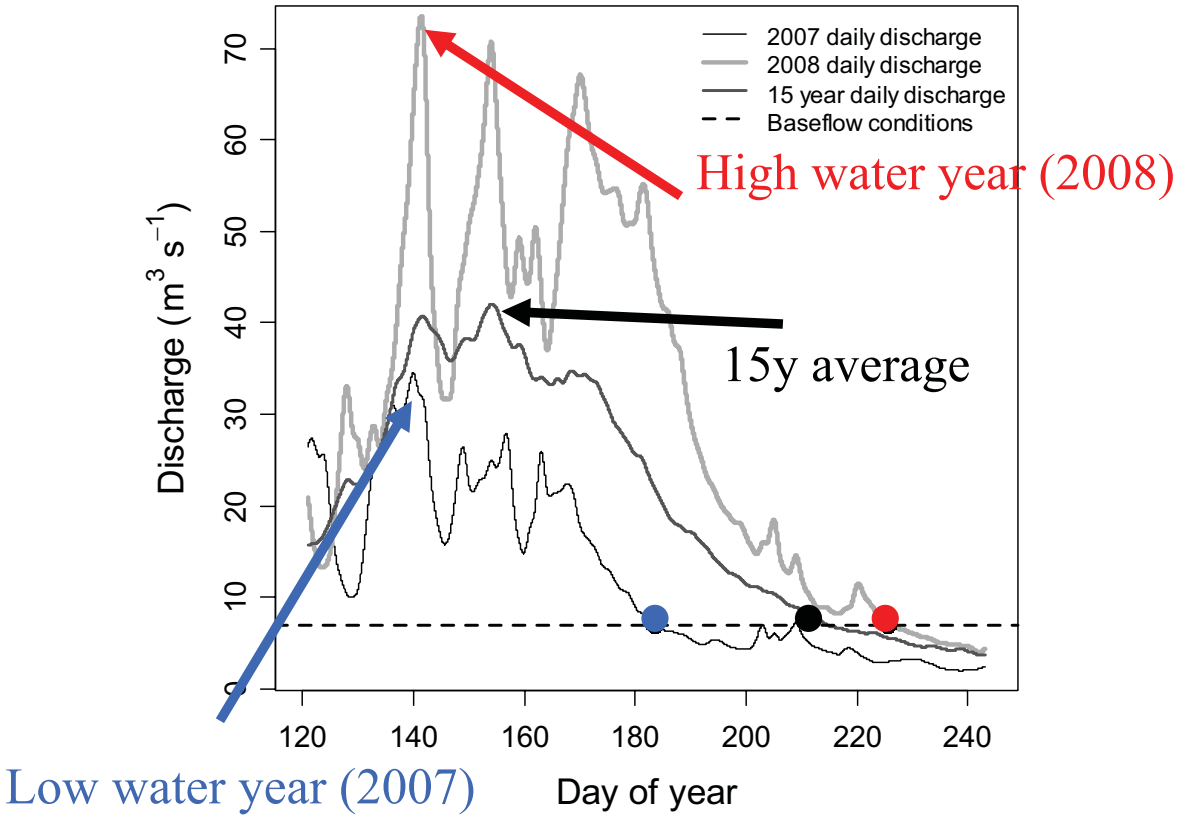



Fig. 31. Discharge from USGS gauging station (09112200) on the East River downstream of the confluence of Cement Creek in 2007, 2008 and the 15-year average (01-May to 31-Aug). The dashed line (`7m³ s⁻¹) approximates baseflow conditions. Arrows point to peak flows and dots (●) on the hydrographs indicate the dates when baseflow began in 2007 (blue), 2008 (red) and the 15y average (black). (Modified from Fuller and Peckarsky 2011.)

sites has the potential to limit recruitment and threaten the future of these mayfly populations.


## Acknowledgements

We thank our other collaborators and students who have contributed important parts of this story: Brad Taylor, Matt Harper, Matt Fuller, Maruxa Álvarez, Wendy Brown, Marge Penton, Steve Horn, Chris Caudill, Mark McPeek, Cathy Cowan, Dave Lytle, Chester Anderson and Jonas Dahl. Also thanks to Lauren Culler (and the other grad student members of the committee that organized the symposium) for inviting BLP to present a talk at the 2010 Meetings of the Entomological Society of America, on which this paper is based. This work was primarily supported by multiple grants to BLP from the National Science Foundation.


## References Cited


**Allan, J. D. 1978.** Diet of brook trout (*Salvelinus fontinalis* Mitchill) and brown trout (*Salmo trutta* L.) in an alpine stream. Verh. Internat. Verein Limnol. 20: 2045-2050.

**Allan, J. D. 1981.** Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. Can. J. Fish. Aquat. Sci. 38: 184-192.

**Bengtsson, J. 1982.** Oviposition behavior and egg hatching in *Baetis rhodani* Ephemeroptera. Flora Fauna. 88: 27-34.

**Blaustein, L. and B. P. Kotler. 1993.** Oviposition habitat selection by the mosquito *Culiseta longiareolata*: effects of conspecifics, food and green toad tadpoles. Ecol. Entom. 18: 104-108.

**Brittain, J. E. 1982.** Biology of mayflies. Annu. Rev. Entom. 27: 119-147.

**Bryant, E. H. 1969.** A system favoring the evolution of holometabolous development. Ann. Entom. Soc. Amer. 62: 1087-1091.

**Canyon, D.V., J. L. K. Hii, and R. Muller. 1999.** Adaptation of *Aedes aegypti* (Diptera: Culicidae) oviposition behavior in response to humidity and diet. J. Ins. Physiol. 45: 959-964.

**Caudill, C. C. 2003.** Empirical evidence for nonselective recruitment and a source-sink dynamic in a mayfly metapopulation. Ecology 84: 2119-2132.

**Caudill, C.C. and B.L. Peckarsky. 2003.** Lack of behavioral or developmental responses by mayfly larvae to trout predators. Ecology 84: 2133-2144.

**Craig, T. P., J. K. Itami, and P. W. Price. 1989.** A strong relationship between oviposition preference and larval performance in a shoot galling sawfly. Ecology 70: 1691-1699.

**Damman, H. and N. Cappucino. 1991.** Two forms of egg defense in a chrysomelid beetle: egg clumping and excrement cover. Ecol. Entom.16:163-167.

**Eaton, A. E. 1888.** A revisional monograph of the recent Ephemeridae or mayflies. Trans. Linn. Soc. 2: III.

**Elliott, J. M., and U. H. Humpesch. 1980.** Eggs of Ephemeroptera. Annu. Rep. Freshwater Biol. Assoc. 48:41-52.

**Encalada, A. C. 2005.** Patterns, mechanisms and consequences of selective oviposition behavior of the mayfly *Baetis bicaudatus* in Colorado high-altitude streams. Ph.D. Thesis, Cornell University, Ithaca.

**Encalada, A. C., and B. L. Peckarsky. 2006.** Selective oviposition behavior of the mayfly *Baetis bicaudatus*. Oecol. 148: 526-537.

**Encalada, A. C., and B. L. Peckarsky. 2007.** A comparative study of the cost of alternative mayfly oviposition behaviors. Beh. Ecol. and Sociobiol. 61: 1437-1448.

**Encalada, A. C., and B. L. Peckarsky.** The influence of recruitment on within-generation population dynamics of the mayfly *Baetis bicaudatus* in fish and fishless streams. In press.

**Fuller, M. R., and B. L. Peckarsky. 2011.** Ecosystem engineering by beavers affects mayfly life histories. Freshw. Biol. 56: 959-979.

**Harker, J. 1989.** Mayflies. Naturalists' Handbooks 13. Richmond Publishing Co. Ltd. Sough, England.



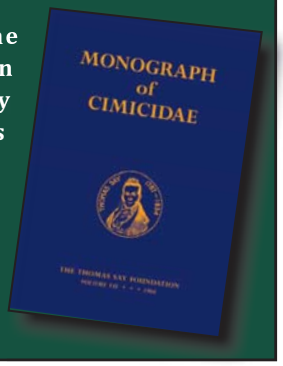

Downloaded from http://ae.oxfordjournals.org/ by guest on April 29, 2016

**Harper, M. P., and B. L. Peckarsky. 2006.** Emergence cues of a mayfly in a high altitude stream ecosystem: Implications for consequences of climate change. Ecol. Appl. 16: 612-621.
**Hinton, H. E. 1981.** Biology of insect eggs. Vol I, II, III. Pergamon Press, Oxford, New York.
**Juliano, S. A., G. F. O'Meara, J. R. Morrill, and M. M. Cutwa. 2002.** Desiccation and thermal tolerance of eggs and the coexistence of competing mosquitoes. Oecol. 130: 458-469.
**Kohler, S. L. 1984.** Search mechanism of a stream grazer in patchy environments: the role of food abundance. Oecol. 62: 209-218.
**Kouki, J. 1991.** Tracking spatially variable resources: an experimental study on the oviposition of the water-lily beetle. Oikos 61: 243-249
**McKnight D. 2001.** Freshwater ecosystems and climate change: recent assessments and recommendations. Limnol. Oceanog. Bull. 10: 61-65.
**McMillan, V. E. 2000.** Aggregation behavior during oviposition in the dragonfly *Sympetrum vicinum* (Hagen) (Odonata: Libellulidae). Am. Midl. Nat. 144: 11-18.
**McPeek, M. A., and B. L. Peckarsky. 1998.** Life histories and the strengths of species interactions: combining mortality, growth and fecundity effects. Ecology 79: 235-247.
**Michiels, N. K., and A. A. Dhondt. 1990.** Costs and benefits associated with oviposition site selection in the dragonfly *Sympetrum danae* (Odonata, Libellulidae). Anim. Behav. 40: 668-678.
**Morgan, A. H. 1911.** Mayflies of Fall Creek. Ann. Entomol. Soc. Amer. 4: 93-119.
**Murphy, H. E. 1922.** Notes on the biology of some of our North American species of may-flies. II Notes on the biology of the may-flies of the genus *Baetis.* Lloyd Library Bull. 22: 40-42.
**Needham, J. G., K. J. Morton, and O. A. Johannsen. 1905.** Mayflies and midges of New York. Bull. 86. Entomol. 23. New York State Education Department, Albany.
**Ohgushi, T. 1992.** Resource limitation on insect herbivore populations, pp. 199-241. *In* Hunter M.D., Ohgushi T., Price P.W. (eds). Effects of resource distribution on animal-plant interactions. Academic Press, San Diego,.
**Ohgushi, T. (1995).** Adaptive behavior produces stability in herbivorous lady beetle populations, pp. 202-319. *In* N. Cappuccino and P. W. Price (eds), Population dynamics: New approaches and synthesis. Academic Press, Sand Diego.
**Otto, C., and B. S. Svensson. 1981.** Why do *Potamophylax cingulatus* (Steph) (Trichoptera) larvae aggregate at pupation? pp. 285-292. *In* G. P. Moretti (ed). Proc. 3rd Internat. Symp. Trichoptera, Vol. 20. Dr. W. Junk Publishers, The Hague.
**Peckarsky, B.L. 1991.** Habitat selection by stream-dwelling predatory stoneflies. Can. J. Fish. Aquat. Sci. 48: 1069-1976.
**Peckarsky, B. L., C. A. Cowan, M. A. Penton, and C. Anderson. 1993.** Sublethal Consequences of Stream-Dwelling Predatory Stoneflies on Mayfly Growth and Fecundity. Ecology 74: 1836-1846.
**Peckarsky, B. L. 1996.** Alternative predator avoidance syndromes in stream-dwelling mayflies. Ecology 77: 1888-1905.
**Peckarsky, B. L., and A. R. McIntosh. 1998.** Fitness and community consequences of avoiding multiple predators. Oecol. 113: 565- 576.
**Peckarsky, B. L., B. W. Taylor, and C. C. Caudill. 2000.** Hydrologic and behavioral constraints on oviposition of stream insects: implications for adult dispersal. Oecol. 125: 186-200.
**Peckarsky, B. L., B. W. Taylor, A. R. McIntosh, M. A. McPeek, and D. A. Lytle. 2001.** Variation in mayfly size at metamorphosis as a developmental response to risk of predation. Ecology 82: 740-757.
**Peckarsky, B. L., A. R. McIntosh, B. W. Taylor, and J. Dahl. 2002a.** Predator chemicals induce changes in mayfly life history traits: A whole-stream manipulation. Ecology 83: 612-618.
**Peckarsky, B. L., A. R. McIntosh, C. C. Caudill, and J. Dahl. 2002b.** Swarming and mating behavior of a mayfly *Baetis bicaudatus* suggest stabilizing selection for male body size. Behav. Ecol. Sociobiol. 51: 530-537.
**Price, P. W. 1994.** Phylogenetic constraints, adaptive syndromes, and emergent properties: from individuals to population dynamics. Res. Popul. Ecol. 36:3-14.
**Price, P. W., and T. Ohgushi. 1995.** Preference and performance linkage in a *Phyllocolpa* sawfly on the willow, *Salix miyabeana*, on Hokkaido. Res. Pop. Ecol. 37: 23-28.
**Price, P.W., T. P. Craig, and M. D. Hunter. 1998.** Population ecology of a gall-inducing sawfly, *Euura lasiolepis*, and relatives, pp 324-340. *In* J. P. Dempster, and I. F. G. Mc Lean IFG (eds), Insect Populations, 1st edn. Kluwer Academic Publishers, Dordrecht.
**Rausher, M. D. 1979.** Egg recognition: its advantage to a butterfly. Anim. Behav. 27: 1034-1040.
**Reich, P., and B. J. Downes. 2003.** The distribution of aquatic invertebrate egg masses in relation to physical characteristics of oviposition sites at two Victorian upland streams. Freshw. Biol. 48: 1497-1513.
**Resetarits, W. J. 1996.** Oviposition site choice and life history evolution. Amer. Zool. 36:205-215.
**Resetarits, W. J. 2001.** Colonization under threat of predation: avoidance of fish by an aquatic bettle, *Tropisternus lateralis* (Coleoptera: Hydrophilidae). Oecol. 129: 155-160.
**Richards, C., and G. W. Minshall. 1988.** The influence of periphyton abundance on *Baetis bicaudatus* distribution and colonization in a small stream. J. North Am. Benthol. Soc. 7: 77-86.
**Sadegui, H. and G. Gilbert. 1999.** Individual variation in oviposition preference, and its interaction with larval performance in an insect predator. Oecol. 118: 405-411.
**Siva-Jothy, M.T., D. W. Gibbons, and D. Pain. 1995.** Female oviposition-site preference and egg hatching success in the damselfly *Calopteryx splendens xanthostoma*. Behav. Ecol. Sociobiol. 37: 39-44.
**Smith, R. L. 1976.** Male brooding behavior of the water bug *Abedus herberti* (Hemiptera: Belostomatidae). Ann. Entomol. Soc. Am. 69: 740-747.
**Spencer, M., L. Blaustein, J. E. Cohen. 2002.** Oviposition habitat selection by mosquitoes (*Culiseta longiareolata*) and consequences for population size. Ecology 83: 669-679.
**Thompson, J. N. 1988.** Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Entomol. Experim. Appl. 47: 3-14.
**Thompson, J. N., and O. Pellmyr. 1991.** Evolution of oviposition behavior and host preference in Lepidoptera. Annu. Rev. Entomol. 36: 65-89.
**Wildermuth, H. 1992.** Visual and tactile stimuli in choice of oviposition substrates by the dragonfly *Perithemis moova* Kirby (Anisoptera: Libellulidae). Odonatol. 21: 309-321.
**Wissinger, S. A., W. S. Brown, and J. E. Jannot. 2003.** Caddisfly life histories along permanence gradients in high-altitude wetlands in Colorado (USA). Freshw. Biol. 48: 255-270.

**Bed Bug Book Is Back In Stock!**

**Monograph of Cimicidae, the definitive systematic resource on bed bugs, has been reprinted by ESA. It is available to ESA members for $59.00 (soft cover).**

See http://www.entsoc.org/pubs/books/thomas_say/ThomasSays.htm




**Barbara L. Peckarsky** is an aquatic ecologist who studies streams at the Rocky Mountain Biological Laboratory in western Colorado, USA. She is an emeritus professor at Cornell University and an Honorary Fellow and Adjunct Professor at the University of Wisconsin Madison. **Andrea C. Encalada** is an aquatic ecologist at Universidad San Francisco de Quito and IMAR, and studies aquatic invertebrate behavior and population dynamics. **Angus McIntosh** is the Mackenzie Foundation Chair in Freshwater Ecology at the University of Canterbury in Christchurch, New Zealand. He works on a wide range of topics from freshwater food webs to fish ecology and riparian management, but also has a passion for photography.

Downloaded from http://ae.oxfordjournals.org/ by guest on April 29, 2016